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GAMETIC COUPLING AS A CAUSE OF CORRELATIONS

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WHEN two distinct characters consistently occur together in the offspring of a hybrid, the phenomenon is termed in Mendelian parlance "gametic coupling." If the characters sometimes occur independently, but appear together more frequently than they should by chance, the term "partial gametic coupling" is applied. If the characters occur together less frequently than is to be expected, the condition is termed "repulsion," while if they never occur together in the same individual it is called "spurious allelomorphism."

In mathematical language, characters that show partial gametic coupling are said to be "positively correlated," those that show repulsion, "negatively correlated." If they always occur together in the same individual, the correlation is said to be "perfect" or "complete," while if they never occur together the negative correlation is perfect.

When characters that show a positive correlation or partial gametic coupling are derived from the same parent, they are termed "coherent" by Cook (1909, p. 16). Many of the examples of partial gametic coupling formerly reported in Mendelian literature were probably of this nature, but with the attention focused on the idea that all characters were independent units, the possibility of such coherence was not considered, and it is sometimes not to be determined from the data presented whether the correlated characters were derived from the same or different parents. This phenomenon of coherence, which appears to most field naturalists and practical breeders as a well-known fact, strikes the followers of Mendel as a novel idea, to judge from the following (Bateson & Punnett, 1911, p. 6):

> The fact, however, that the mode in which factors are combined in the original parents can influence the distribution of the factors among gametes of F_1 introduces a new conception into genetic physiology.

The difficulty of "breaking up" combinations of characters has so long been a stumbling block to breeders that to them the conception can hardly be considered new. The suggestion that the number of individuals in which two characters are combined bears a definite relation to the number in which they occur singly is without doubt a direct outgrowth of Mendelian investigations and methods of thought. Perhaps this latest application of mechanical conceptions to biology may stimulate research as did Mendel's original discovery. On the other hand, there are many who think that the application of Mendelian formulæ has already been pursued to an absurd point by the factoring and subfactoring of characters and the assumption of intensifying and inhibiting determinants. Those not already abreast of Mendelian literature are not likely to be impressed with the further refinement that aims to devise formulæ for expressing gametic relations between two of these already complicated Mendelian systems.

In considering the relation between two Mendelian characters four possible combinations are involved. Thus, if A and B be taken to represent the appearance of the two characters, and a and b their non-appearance, these four combinations would be expressed as follows: AB, Ab, aB, and ab. The theory of gametic coupling assumes that an attraction or other unknown relation exists between the determinants of the two characters, which results in their occurring together in gametes more frequently than they occur separately.

There appears to have been a preconceived idea that the ratio between the number of gametes in which the determinants for two characters occurred together and the number in which they were separated would be either as 3:1, or 7:1, or 15:1, ratios that are common in Mendelian inheritance of single characters. The reason for this expectation is not apparent.

The persistence with which it is sought to utilize the numbers 4, 8, 16, etc., representing powers of 2, in the interpretation of correlations reminds one of the arguments used at the dawn of science to bring all natural phenomena into some relation with the numbers 4 and 7. Galileo's suggestion that there were more than seven planets was answered by Lizzi:

> There are seven windows in the head, two nostrils, two eyes, two ears, and a mouth, so in the heavens are there two favorable stars, two unpropitious, two luminaries, and Mercury alone undecided and indifferent. From which and many other similar phenomena of nature, such as the seven metals, etc., which it were tedious to enumerate, we gather that the number of planets is necessarily seven. (Snyder, 1907, p. 203.)

The levity of the comparison disappears when one seeks a reason for assuming that the number of gametes in which the characters occur together will be to the number of gametes in which they occur apart as 7:1 or 15:1 or 31:1, etc., and not some intermediate proportion.

In the following pages an attempt is made to review briefly the experiments which have been advanced as proof that the various degrees of correlation fall into this definite series.

The first attempt to refer the correlation of characters to definite differences in the gametes was made by Bateson, Saunders, and Punnett (1906, p. 9) in explaining observed correlations between purple flower color and long pollen grains in hybrid sweet peas.

> . . . A close approach to the Observed F_2 numbers would be given

by a system in which each 16 gametes were composed, thus: $7AB + 1aB + 1Ab + 7ab$, where A is long pollen and a round pollen.

	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
Observed	1,528	106	117	381	1,199	394
Calculated	1,448.5	122.7	122.7	401.5	1,220.5	407.4

The numbers under "White" may be disregarded in this connection since the distribution of long and round pollen grains in this group shows a close approach to the normal 3 : 1 ratio.

Some of the numbers in the "observed" series are above and some below the corresponding numbers of the "calculated" series. That the calculated series approximates the observed series is obvious, but there is no way of determining the degree of this approximation. No method has been proposed for making definite comparisons between such series of numbers. Without some standard of comparison it is difficult to see that anything is gained by resorting to gametic formulæ to represent the degrees of association between characters.

A customary and direct method of comparing the degrees of relationship that exists between any two characters is to compute the coefficient of correlation or Yule's "coefficient of association."

In the following discussion Yule's "coefficient of association" (1900) is used. By this method the complete independence of two character pairs is represented by 0, complete association by 1. Intermediate degrees of relationship are expressed by the intermediate decimals. If the four classes of individuals are represented by a, b, c and d, the coefficient of association is

$$\frac{(a \times d) - (b \times c)}{(a \times d) + (b \times c)}$$

Since this coefficient can be computed directly from the observed numbers the predication of gametic formulæ as a means of expressing degrees of association of characters becomes unnecessary.

With relationships expressed as coefficients of association, probable errors can be calculated. Thus it becomes possible to determine whether the approximations between observed ratios and those calculated from the different gametic formulæ are closer than would result from chance.[1]

The difficulty of securing a 7:1 distribution by dichotomous cell division was appreciated by Bateson and his collaborators in the example first cited. The possibility that the coupling was in an 8:1 ratio was also suggested and kept in mind for a time until a grouping that approximated that resulting from a gametic coupling of a 15:1 ratio was obtained. Regarding the choice between the 7:1 and 8:1 ratios to explain the numbers observed in the first experiment, the authors remarked (Bateson, Saunders and Punnett, 1908, p. 3):

> . . . we are still unable to decide finally between them.

But this indecision was apparently overcome in a subsequent paragraph on the same page. After citing two examples that were referred to a 15:1 ratio, the theory that the couplings follow a definite series was launched in the following statement:

> The undoubted existence of these two grades of gametic coupling in the Sweet Pea suggests that each may find its place in a scheme of increasing intensity of gametic coupling, such as is shown in the accompanying table, where the two allelomorphic pairs are represented by *Aa* and *Bb*:

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[1] Heron has pointed out (1911, p. 109) that the results secured by Yule's formula for the "coefficient of association" do not approximate the true coefficient of correlation, except where the two divisions are near the mean of the entire population. This condition is not met, of course, by characters that occur in one fourth and three fourths of all the individuals. But since the present discussion is confined to examples that approximate the form $3n^2 - (2n - 1) : 2n - 1 : 2n - 1 : n^2 - (2n - 1)$, where $2n =$ the number in the gametic series, they afford a regular sequence and, though the actual values are somewhat arbitrary, they should not be misleading as a means of comparing the degrees of relationship represented by the different gametic formulæ. Thus if the classes observed in an experiment show the same coefficient of association as the classes calculated from some particular gametic ratio, the two series will also give the same coefficient of correlation, though the actual values may differ.

Gametic Series					Zygotes Containing			Neither	
AB	*Ab*	*aB*	*ab*		*A* and *B*	*A* only	*B* only	*A* nor *B*	
1	1	1	1	= 4	9	3	3	1	= 16
3	1	1	3	= 8	41	7	7	9	= 64
7	1	1	7	=16	177	15	15	49	= 256
15	1	1	15	=32	737	31	31	225	=1,024
$n—1$	1	1	$n—1$	$=2n$	$3n^2—(2n—1)$	$2n—1$	$2n—1$	$n^2—(2n—1)$	$=4n^2$

The first term in the series is a simple case of dihybridism in which no coupling exists. The second term we have not yet encountered. But we have an ample series of experimental data which satisfy the third term; and the experimental evidence for the existence of the fourth term rests upon two independent cases.

To facilitate the use of the coefficient of association as a means of determining what gametic ratio most closely approximates observed ratios, Table I has been prepared. This table shows a series of gametic ratios in which the less frequent combinations are taken as 1, and the resulting zygotic series, with the number of individuals that would occur in each of the four classes, followed by the coefficient of association, calculated from the numbers in the zygotic series. The ratios in heavy type are those representing the powers of two to which correlations have been referred under the theory of gametic coupling.

TABLE I

RATIOS OF GAMETIC COUPLING

Gametic Series	Zygotic Series	Coefficient of Association
1 : 1 : 1 : 1	9 : 3 : 3 : 1	.0
2 : 1 : 1 : 2	22 : 5 : 5 : 4	.558
3 : 1 : 1 : 3	**41 : 7 : 7 : 9**	**.766**
4 : 1 : 1 : 4	66 : 9 : 9 : 16	.858
5 : 1 : 1 : 5	97 : 11 : 11 : 25	.905
6 : 1 : 1 : 6	134 : 13 : 13 : 36	.932
7 : 1 : 1 : 7	**177 : 15 : 15 : 49**	**.949**
8 : 1 : 1 : 8	226 : 17 : 17 : 64	.961
9 : 1 : 1 : 9	281 : 19 : 19 : 81	.969
10 : 1 : 1 : 10	342 : 21 : 21 : 100	.975
11 : 1 : 1 : 11	409 : 23 : 23 : 121	.979
12 : 1 : 1 : 12	482 : 25 : 25 : 144	.982
13 : 1 : 1 : 13	561 : 27 : 27 : 169	.985
14 : 1 : 1 : 14	646 : 29 : 29 : 196	.987
15 : 1 : 1 : 15	**737 : 31 : 31 : 225**	**.988**
16 : 1 : 1 : 16	834 : 33 : 33 : 256	.990
31 : 1 : 1 : 31	**3,009 : 63 : 63 : 961**	**.9973**
63 : 1 : 1 : 63	**12,161 : 127 : 127 : 3,969**	**.9993**
127 : 1 : 1 : 127	**48,897 : 255 : 255 : 16,129**	**.9998**

Returning to the consideration of the original example of gametic coupling in the sweet peas, the coefficient of association, .958 ± .004, is seen to be intermediate between that resulting from a 7:1 and an 8:1 ratio.

Notwithstanding the fact that the figures correspond somewhat more closely with an 8:1 than they do with a 7:1 ratio, an evident preference for numbers that are powers of 2 is shown when the possibility of an 8:1 ratio is discussed. Instead of saying that 18 gametes are concerned, the number is spoken of as 16 + 2, and the fact that a ratio of 15:2 would give almost exactly the observed association is not even considered.

The next example of gametic coupling to be reported was in the same series of crosses (Bateson, Saunders and Punnett, 1908, p. 11), where the progeny of four individuals showed the following grouping: 296:19:27:85. This is referred by the authors to the theoretical 7:1 ratio, though it shows almost the same association as an 8:1 ratio, that is, .960. The probable error, .008, would indicate, however, that with this number of individuals such a deviation might easily be due to chance. The numbers are, therefore, too small to afford evidence affecting the choice between a 7:1 and an 8:1 formula.

From the progeny of one of these four individuals consisting of 111 plants and showing an association of .914, 10 individuals showing both dominant characters were selected and propagated. The progeny of the 10 plants taken together gave the following grouping: 493:25:25:138. This grouping is considered only in connection with the 7:1 and 15:1 distribution, though the association .982 ± .004 would indicate that a gametic series of 12:1 would most closely fit the numbers. The deviation from the 7:1 ratio is 9 times the probable error, and from the 15:1 ratio, about twice the probable error.

With respect to the characters considered separately, the classes secured from each of the 10 individuals showed a remarkable conformity to the expected 3:1

ratio. In the degree of association between the characters, however, no such uniformity was exhibited. Leaving out of consideration two families represented by only a few individuals, the coefficient of association varies from .910 to .990. In terms of gametic coupling this shows a range from 6:1 to 16:1, and since the series as a whole accords with a 12:1 ratio it is not apparent why only 7:1 and 15:1 ratios are considered.

Individuals were again selected from two of the families which showed the highest correlation, and grown the following season. The progeny from the first family behaved irregularly and the presence of some disturbing process was suspected, though the deviations with respect to the individual character pairs were less than the probable error.

The second family gave individuals with the following grouping (Bateson, Saunders and Punnett, p. 12): 583:26:24:170 (association .987 ± .0026). Of this it is said:

> It is obvious that the numbers in this group of families accord very closely with the figures expected on a 15 : 1 : 1 : 15 basis, and the view that this is the system actually followed receives confirmation from the distribution of the pollen and color characters in F_2 families from the Bush × Cupid crosses where the following figures were obtained: 131:6:5:42. (Association .989 ± .005.)

Here again when it is said that the figures "accord very closely," it can only be meant that they accord closely with one of the formulæ in the hypothetical series as compared with other members of the series. The numbers are, of course, inadequate to afford evidence as to whether the observed figures accord more closely to those resulting from a 15:1 combination than they do, for example, to a 16:1 or a 14:1, yet the results are taken to support the original assumption that the groupings are in powers of two.

The examples of gametic coupling thus far reported are summarized by Bateson and Punnett as follows (1911, p. 5):

3:1.	No case yet known.
7:1.	*Sweet Pea.* Blue factor and long pollen.
7:1.	*Primula sinensis.* Magenta color and short style.
15:1.	*Sweet Pea.* Fertile anthers and dark axils.
31:1.	No case yet known.
63:1.	*Pisum.* Development of tendrils and round seed.
127:1.	*Sweet Pea.* Blue factor and erect standard.

As we have seen, the first example is closer to an 8:1 ratio. The second example is apparently based on an experiment comprising 47 individuals (Gregory, 1911, p. 12). The classes were 33:3:1:10, and the author states,

> . . . the partial coupling observed is almost entirely certainly of the form 7 : 1 : 1 : 7.

The reason for this assurance is not apparent since the grouping is really nearer to that resulting from a 15:1 ratio. The probable error, .015, is so large, however, that it would be impossible to determine the grade of coupling closer than to say that it probably falls somewhere between 8:1 and 31:1.

The third example referred to the 15:1 ratio appears to be based on 885 individuals showing an association of .993 ± .0017, indicating a coupling of about 20:1, the deviation from the 15:1 association being 2.9 times the probable error.

With respect to the examples where the association is closer, none of the reported experiments have been conducted on a sufficient scale to determine whether the gametic ratios that are multiples of two are approximated more closely than other ratios. One of the most exact approximations thus far reported is that of Vilmorin and Bateson (1911, p. 10) where the numbers 319:4:3:123 (association .9994 ± .0003) were obtained. This is certainly a close approximation to the figures that would result from a gametic coupling of 63:1:1:63, which for this number of individuals would be 333.27:3.48:3.48:108.77. Yet the observed numbers can be still more closely approximated by assuming that the coupling was in the proportion of 75:1, which would give the figures 334.57:2.98:2.98:109.47. The observed numbers are somewhat closer to the 63:1 than to the 127:1, the proportion next above in the proposed series. But why avoid the intermediates?

It should be kept in mind that the series was built up in the first place, not because the observed numbers agreed with some member of this series more closely than was to be expected by the laws of chance, but apparently for *a priori* reasons, because the numbers in this series were in accord with the Mendelian ratios for the appearance of single characters which represent powers of 2.

When the correlation is as high as in the above example it would require, not hundreds of individuals, but tens of thousands to prove that the observed numbers were in accord with those resulting from any particular gametic ratio. In the experiment referred to the 61:1 ratio, there are two classes represented by 4 and 2 individuals, respectively. A change of two or three individuals in each of these classes would cause the array to correspond as closely with a 31:1 or 127:1 ratio as it now does with the 63:1.

In the very nature of things any observed association must fall nearer to some one of the calculated ratios than to any other, yet in the discussion of these experiments this seems not to have been appreciated. The data would have supported in the same way any other choice of preferred ratios.

COHERENT CHARACTERS IN HYBRIDS OF CHINESE MAIZE

Beginning in 1908, experiments have been conducted with a variety of maize secured from China. The endosperm of this Chinese variety is of a peculiar waxy texture, a character thus far not reported in any other variety.

There are two strains of the Chinese variety, one white, the other with colored aleurone. In a series of hybrids between Chinese and American varieties made by Mr. J. H. Kempton and the author, the waxy character was found to be definitely recessive in the first generation. In the second generation the character reappears apparently unchanged in slightly less than 25 per cent. of the individual seeds.

Crosses between white Chinese and colored American, and colored Chinese and white American showed a pronounced coherence between the texture of the endosperm and the color of the aleurone layer.

Results of the first season's work in this field were reported at the International Conference of Genetics in Paris, 1911. At that time no attempt was made to determine the gametic ratios necessary to account for the observed correlations.

In these crosses the characters segregate with definitely alternative expression, but the classes seldom show simple Mendelian ratios. In only one cross were two of the four classes even approximately equal.

In the results of the next season's work there were five additional ears sufficiently near the 3:1 ratio in both characters to be considered from the standpoint of gametic coupling. The data derived from these five ears, and from the one of the previous season, are shown in Table II.

TABLE II

Ear No.	No. Seeds	Colored Horny	Colored Waxy	White Horny	White Waxy	Coefficient of Association	Deviation from Coefficient of 3:1 Ratio	Deviation in Terms of Probable Error
152	183	112	20	22	29	.761 ±.049	.005	0.10
301	579	372	62	63	82	.773 ±.029	.007	0.24
302	536	343	52	53	88	.833 ±.024	.067	2.79
303	627	409	57	62	99	.839 ±.021	.073	3.48
325	650	434	55	61	100	.856 ±.019	.090	4.74
380	161	104	17	18	22	.764 ±.058	.002	0.03
Total	2736	1774	263	279	420	.821 ±.011	.055	5.00

The ratios obtained in these six cases might be hailed as a prediction fulfilled, since in every case the numbers approximated those that would result from a 3:1:1:3 ratio, which has remained a gap in the theoretical series.

In three of the six ears the deviation from the correlation resulting from a 3:1 ratio is less than the probable error. The deviation for the total is less than three times the probable error, and might readily be only a chance deviation. In two of the ears, however (Nos. 303 and 325), the deviations are rather large to be ascribed to chance.

In view of the fact that previously reported experiments fail to show an equally close approximation to other members of the proposed series, there is no adequate reason for assuming that the present approximation to the numbers of a 3:1 ratio belongs to a series of formulæ represented by the powers of 2. That no such regularity exists in the interrelation of different character pairs is more definitely demonstrated by the experiments described below. These results indicate that the association of characters may be determined after the conjugation of the gametes.

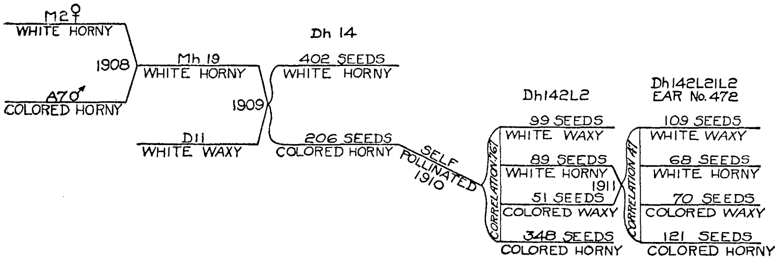
COHERENCE OF CHARACTERS NOT ALWAYS THE RESULT OF GAMETIC DIFFERENCES

If correlations are in all cases due to gametic differences, there should be no correlations exhibited in a cross with a Mendelian formula $Aabb \times aabB$. In our experiments with corn this would be represented by a cross between colored-waxy and white-horny, where the first is heterozygous in aleurone color and the second heterozygous in endosperm texture. The colored aleurone is dominant to white, and the horny endosperm to the waxy. If colored aleurone is represented by C, white aleurone by *c*, horny endosperm by *H*, and waxy endosperm by *h*, the gametic structure would be as follows: Female parent, *cchH*, producing two classes of gametes, *ch* and *cH*; male parent, *Cchh*, producing gametes *Ch* and *ch*. In neither case is there opportunity for coupling in the gametes since in the female parent all of the gametes should bear the white character, and those of the male parent the waxy character. The significance of crosses of this nature was not realized at the time pollinations were being made, and but 5 ears of this kind were secured. In two of these ears there is a significant correlation. The classes exhibited in the five ears are shown in Table III.

TABLE III

Ear No.	No. Seed	Per Cent. White	Per Cent Waxy	White Waxy	White Horny	Colored Waxy	Colored Horny	Coefficient of Association
472	505	30.1	46.4	91	61	143	210	.373 ±.057
471	368	48.	48.6	109	68	70	121	.47 ±.056
314	283	44.5	52.7	65	61	84	73	−.038 ±.081
272	395	61.2	47.1	122	120	64	89	.171 ±.068
256	141	46.8	48.9	27	39	42	33	−.295 ±.105

The two ears in which the correlation appears significant (Nos. 471 and 472) have a common ancestry, different from that of the other ears. The history of these ears is as follows: In 1908 a plant of a white Mexican variety was pollinated by a Hopi variety with colored aleurone, producing a pure white ear, *Mh*19. In 1909 a plant from *Mh*19 was pollinated by white Chinese, the variety possessing the waxy endosperm. The resulting ear *Dh*14 had white and colored seed in the proportion of 2 white to 1 colored, with no trace of the waxy endosperm. In 1910 a plant from a colored seed of *Dh*14 was self-pollinated, producing an ear *Dh*142*L*2 with the following classes: white-waxy 99, white-horny 89, colored waxy 51, colored horny 348. This represents an association between colored and horny of .767, almost exactly that expected on a coupling ratio of 3:1, but it will be



noticed that the two middle classes are not equal. In 1911 two plants grown from white horny seeds of *Dh*142*L*2 were pollinated by a plant from a colored waxy seed of the same ear, producing the two ears, Nos. 471 and 472. The pedigree of these two ears is graphically shown in Diagram 1.

The plants which bore ear 472 bore also a second ear which was self-pollinated. Contrary to expectation, this ear showed slight traces of aleurone color. That there was a tendency to produce aleurone color in this extracted recessive is also indicated by the low percentage of the total white seeds in ear 472, which is 30 instead of 50.

With ear 471 there is every indication that one of the parents was homozygous with respect to the recessive color character and the other with respect to the texture of the endosperm. A self-pollinated second ear from the plant that produced ear 471 had 24 horny seeds and 5 waxy, all of them white. A self-pollinated ear was also secured from the plant which was the male parent of both 471 and 472. This ear had 31 white seeds and 128 colored, all of them waxy. The total percentage of white seeds in ear No. 471 was 48, a close approximation to the expected 50.

The nature of this experiment seems to preclude the application of the theory of gametic coupling which would explain correlations by assuming attractions or repulsions between the character determinants in the gametes. While attractions which might cause some combinations to be represented by larger numbers of gametes would disturb the Mendelian ratios, they could not produce the effect of correlation or coherence of characters.

Thus the female parent might produce more gametes bearing white and waxy than it did colored and waxy, or there might be a greater fatality among the colored waxy gametes. Any such disparity in the classes of the gametes would result in more than 50 per cent. of the zygotes showing the recessive characters, but even so, there would be no correlation.

On the presence and absence hypothesis, a positive correlation between two dominant characters like aleurone color and horny texture must be considered a different phenomenon from a positive correlation between color and waxy texture (Bateson, 1909, pp. 151, 158). The first case has to be looked upon as an example of attraction, the second of repulsion. This appears an unnecessary complication, as Emerson (1911, p. 79) has pointed out. The significant fact would seem to be that both cases may be considered as examples of coherence.

Appreciation of the fact that many of the cases of gametic coupling are examples of coherence makes any assumed regularity in the degree of correlation still more absurd. But in spite of cases of coherence that result in reversal of correlation, the idea that the characters are represented by material particles that remain unchanged by association in the zygote continues to be held. To preserve the conception of pure unit characters, theories of positional relations of unit characters are now being proposed. Simple Mendelian ratios can also be explained by positional relations of character determinants as well as by theories of alternative transmission (Swingle, 1898; Cook, 1907, p. 353), and this view has the advantage that it can accommodate facts which indicate a complete transmission of characters.

A theory to explain how positional relations of determinants in the chromosomes may be responsible for the phenomenon of coherence has been proposed by Morgan (1911). The suggestion is that coupled or positively correlated characters may lie close together in the chromosome and that in the conjugate generation pairs of chromosomes are twisted around each other. If, as claimed, the chromosome pairs split in a single plane, characters which lie close together in the original chromosomes would seldom be separated, while characters remote from each other in the chromosome would stand an even chance of being separated.

If the position of the various determinants in the chromosomes is definite, only slight variations in the degree of association among hybrids between the same parental strains would be expected, but there would be no reason to expect that the different degrees of correlation should fall into a definite series.

SELECTIVE POLLINATION

From the standpoint of complete segregation or alternative inheritance of characters there remains the possibility of correlations being the result of selective pollination. It is conceivable that the ovules which bear one of the segregating characters are more readily fertilized by pollen bearing another character with which it was associated in the parent. As applied to our own experiments, ovules which are potentially waxy might be more readily fertilized by pollen which is potentially white.

If correlations are the result of selective pollination, no correlation should be shown as the result of crossing an individual that is heterozygous with respect to both of the character pairs with an individual showing both of the recessive characters, for in such a cross the gametes of one parent would be all of one kind. In our own experiments, crosses between plants from hybrid seed showing horny endosperm and colored aleurone (both dominant characters) with plants from white waxy seeds (both recessive characters) should throw light on this point.

If the correlations result from numerical inequalities in the classes of the gametes, the seed classes resulting from such a cross as that described above should be the same as the gametic classes produced by the heterozygous parent. Thus, if the seed classes in a self-pollinated ear correspond to those expected from a 3:1 ratio, the same plant when crossed with a plant showing both recessive characters should show classes in the ratio, 3 white-waxy, 1 white-horny, 1 colored-waxy, and 3 colored-horny. On the other hand, if the correlations result from selective pollination, no correlation should appear in such a cross since the pollen is all of one kind. Ears that represent crosses of this kind are described in Table IV. It will be seen that in all of the seven ears there is a significant correlation.

TABLE IV

Ear No.	No. Seeds	Colored Horny	Colored Waxy	White Horny	White Waxy	Coefficient of Association
144	600	125	40	232	203	.464 ± .054
250	245	19	74	104	48	−.788 ± .040
251	377	52	29	138	158	.345 ± .077
390	458	115	35	94	214	.764 ± .032
391	231	65	10	49	107	.868 ± .032
392	316	84	16	68	148	.840 ± .051
401	518	3	29	263	223	−.839 ± .061

It is interesting to note that in two ears, Nos. 250 and 401, while the correlation is relatively high, it is reversed; *i. e.*, the positive correlation is between colored aleurone and waxy endosperm instead of between colored aleurone and horny endosperm as was the case in the original F_2 ears. Whether the correlation is positive or negative does not affect its use as evidence in eliminating the possibility of selective pollination, so long as the correlation is significant. From the standpoint of the presence and absence hypothesis, the coupling or attraction has given place to a repulsion.

The results shown in Tables III and IV indicate that the association of different characters may be determined at different stages in the ontogeny of the individual, much as the appearance or non-appearance of a simple character may occur at different times in the life history. Thus in ears 471 and 472, Table III, the correlated characters must have become associated after the formation of the gametes, while the absence of positive correlation in ears 314 and 317 of the same table shows that in these ears where associations in the gametes were excluded no correlations were subsequently produced. The results in Table IV further show that excluding the possibility of selective pollination did not prevent the appearance of significant correlations. It appears no more reasonable to assume that the number of individuals that are to show a particular combination of characters is always determined at the time the gametes are formed, than it would be to argue that the number of nodes destined to bear a juvenile type of foliage are definitely determined at this time.

The theory of gametic coupling advanced by Bateson and Punnett leads them (1911, p. 6) to entertain the idea that, while segregation is definite and complete, the apparently significant cytological processes of maturation may have nothing to do with the phenomenon. These authors would have the association of characters determined before the maturation divisions.

> Now that we know of a series involving as many as 256 terms (127 + 1 + 1 + 127) it is most difficult to conceive that such a system can be produced in the maturation-divisions of the ovarian tissue of such a plant as a sweet pea. We may well be tempted to look much earlier in the developmental processes for the establishment of these differentiations, and it is not impossible that they may be established as early as the embryonic constitution of the sub-epidermal layer itself.

The suggestion that segregation occurs early in the ontogeny of the individual was apparently occasioned by the belief in the definiteness of the mathematical relations between different character pairs. As we have seen, there is little evidence for this belief. The correlation shown in ear 471, Table III, affords a definite indication that such associations of characters may be formed after the production of the gametes.

Even though the definite and material segregation of characters be maintained, all grades of correlation could still be determined during the two nuclear divisions that follow synapsis. The process might be looked at as follows:

When two character pairs are involved in a hybrid, the tetrads resulting from the different mother cells would all be of three types with respect to the two characters involved: (I) *AB, AB, ab, ab;* (II) *AB, Ab, ab, aB;* (III) *Ab, Ab, aB, aB.* Each of these fulfills the condition deemed necessary from a Mendelian standpoint, that two daughter cells of each tetrad receive the dominant and two the recessive determinants. Where *A* and *B* are correlated, it may be assumed that tetrads represented by (III) are not formed. If the two remaining kinds were produced in equal numbers, a gametic ratio of 3:1:1:3 would result. By the formation of two mother cells of type I for every one of type II, a ratio of 5:1:1:5 would result. The formation of these two types of mother cells in different proportion would provide for all degrees of correlation.

Additional examples of gametic coupling, some of which, at least, are in the nature of coherences, are reported by Gregory (1911, *B*, p. 128). As in our experiments with hybrids of Chinese maize, examples of gametic coupling were encountered of a lower order than 3:1:1:3, the lowest ratio in the theoretical series. Even this discovery did not result in his questioning the validity of the hypothesis. A further refinement was devised to accommodate the results. Advantage was taken of the possibility that the gametic coupling may exist in only one sex:

> For the time being it may be pointed out that a very close approximation to the observed numbers is given by the assumption that a coupling of the form 7 : 1 : 1 : 7 is present in gametes of one sex only, gametes of the opposite sex being produced in equal numbers of all four kinds.

In such a case, a gametic coupling of the 7:1 in one sex, with all classes equally represented in the other sex, would result in an association of .542, slightly lower than that resulting from the ordinary 3:1 ratio. By a similar fractioning of the 3:1 ratio, the series can be provided with a still lower member, with an association of .390.

In all recently reported experiments the reality of the proposed series of ratios seems to be taken for granted and results are viewed only from this standpoint.

It is hoped that the previous discussion may operate to check this practise of referring examples of coherence to preconceived gametic ratios without considering the possibility that an apparent agreement may be only a chance approximation.

So long as the preconceived series is taken for granted and intermediates are not considered, the results of all experiments will seem to give additional evidence in support of the series.

We have seen that the results of previously reported experiments do not correspond to the ratio in the expected series more closely than they do to others that are intermediate, and furthermore that in some cases, at least, the associations are not due to relations of the determinants inside the gametes at all, but occur after the stage of karyapsis, or nuclear fusion, has been reached (Cook and Swingle, 1905).

SUMMARY

The theory of gametic coupling assumes that correlations between two Mendelian character pairs are caused by attractions or repulsions between character-units or determinants, previous to the formation of the germ cells. These attractions or repulsions are supposed to increase the number of gametes bearing certain combinations of determinants.

The further assumption that the various degrees of association observed between different character-pairs will fall into a regular series represented by powers of 2, as in simple Mendelian hybrids, appears to have been accepted without adequate analysis of the data on which it was based.

An examination of the early examples shows that it was only by neglecting the possibility of intermediate ratios, and thus begging the question, that the observed numbers could be said to agree with those of the proposed series.

The lack of any standard or method for making quantitive comparisons between observed and expected series has made it impossible to determine the degree of the supposed approximations. Yule's coefficient of association is proposed as a criterion of comparison, and to make possible the determination of probable erors.

In several cases correlations have been found to be reversible, depending on the way the characters were combined in the parents. This fact has further complicated the theory of gametic coupling, making it necessary to assume that characters which at one time attract each other, at others exhibit repulsion.

In hybrids between Chinese and American varieties of maize coherence has been found between the texture of the endosperm and the color of the aleurone layer. In a few cases, the degree of the correlation approached very closely to that expected from a gametic coupling in a 3:1 ratio (Table II).

Correlations were found in crosses of the Mendelian form $Aabb \times aabB$ (Table III). Such correlations are held to indicate that in some cases at least, the correlation between the characters must be determined after the formation of the gametes.

On the other hand, correlations resulting from crosses of the form $AaBb \times aabb$ eliminate the possibility of selective pollination as a general cause of correlations (Table IV).

The general conclusion is reached that associations between characters, like the appearance of single characters, may rise at different stages in the ontogeny of the individual.

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